

Effect of environmental factors on the abundance variations of two native rodents in agricultural systems of Buenos Aires, Argentina

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Abstract Our aim was to assess the effect of environmental factors on short temporal abundance variations of the two most abundant native rodents of agricultural agroecosystems, *Akodon azarae* and *Calomys laucha*. We conducted a 3-year longitudinal sampling of rodents, and recorded meteorological data such as temperature and precipitation, predation rate by *Leopardus geoffroyi*, *Tyto furcata* and *Athene cunicularia*, vegetation cover and height, characteristics of cropfields and their borders. The effect of these factors on rodent abundance was evaluated through generalized linear mixed models. Abundance variations of both rodent species were explained by characteristics of both cropfields and their borders. At the studied temporal scale, meteorological variables did not have a direct effect on abundance variations, but probably influenced through vegetation characteristics and were expressed in seasonal variations. For *A. azarae* there was also an effect of predation by *L. geoffroyi* (positive) and *T. furcata* (negative), while predation by *A. cunicularia* did not contribute to explain abundance variations of any species.

Key words: environment, GLMM, populations, predation, rodents.

INTRODUCTION

The causes of numerical fluctuations are one of the main questions in population ecology, just like the factors underlying multiannual population cycles and outbreaks (Jaksic 2001; Lima *et al.* 2001). It was suggested that discrepancies in outbreaks topology among different species, as lemmings and voles, are related to different trophic interactions, with interactions with food resulting in more irregular outbreaks than interactions with predators. Other hypotheses propose that different dynamics may result from different sensitivities to climatic factors that may cause irregular fluctuations (Ims *et al.* 2011). There are many studies that describe population dynamics of rodents for the Northern hemisphere (e.g. Hansen *et al.* 1999; Hanski *et al.* 2001; Krebs 2013) but little is known about the Neotropical region. Most of these latter studies have focused on multi-year population dynamics of rodents of arid and semiarid regions of Chile (Lima & Jaksic 1998; Lima *et al.* 1999) and central Argentina (Andreo *et al.* 2009a,b). These multi-year fluctuations were associated to both direct

and indirect (through the abundance of resources) effects of climatic factors, which in temperate areas are also responsible of the seasonal variation in abundance (Jaksic 2001; Jaksic & Lima 2003). Associated to the large temporal scale of these studies there was also a coarse grained spatial scale, which did not take in account spatial heterogeneity, as is caused by intensive agricultural activities. Processes associated to the patterns of abundance variation at small temporal and spatial scales may increase their importance in anthropic systems subject to frequent perturbations, and probably differ from those associated to larger scales.

In rural ecosystems, rodent dynamics are not only affected by natural variables, such as climatic variations, but are also influenced by land use. In terrestrial ecosystems, a great proportion of land is actually devoted to agriculture (Paruelo *et al.* 2005) which has caused major changes in landscapes, with a loss, deterioration and fragmentation of habitats for wildlife (Singleton *et al.* 2003; Massawe & Makundi 2011). Ecological compensation areas as wildflower strips have been widely promoted to decrease the negative effects of farming on wildlife. Since these areas were also shown to contain large numbers of

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small mammals, there is concern about negative effects from dispersal of pest species into adjacent cropfields (Briner *et al.* 2005). Most small mammal research in agrarian landscapes focused on crop damage and rodent control, while little is known about the short-term impact of farming practices on population dynamics and demography (Jacob 2003). Besides the effect of agriculture at large scales (landscapes and ecosystems), at smaller scales populations are affected by the type of crops, level of human disturbance and the relative area covered by crops and less disturbed habitats (Gehring & Swihart 2003; Courtalon & Busch 2010; Fraschina *et al.* 2012). These effects may be direct, as the mortality caused by agrarian disturbance (Tew & Macdonald 1993), or may act indirectly through changes in food resources, plant cover and predation risk (Jacob 2003).

In Pampean agroecosystems, rodent populations show irregular fluctuations among years related to precipitation patterns and temperature, and their effect on winter survival and resource availability during the reproductive season (Fraschina *et al.* 2012). The seasonal pattern is associated to temperature variations that limits the reproductive period and also affects winter survival. Land use also influences seasonal density variations, depending on the phenology of crops (winter or summer crops). During the last decades, land use changed and agriculture expanded in the Pampa (Ghersa & León 1999; Balsa 2001; Bilenca & Miñarro 2004). Along with an expansion of the area, there was a replacement of crops, with a decrease in winter crops as wheat and linen and summer crops as sunflower and maize and an increase in soybean. The cultivation of soybean is now mainly conducted through non tillage labours, and implies an extensive use of herbicides (Andrade *et al.* 2015; Urcola *et al.* 2015). This type of management in the Rolling Pampas modifies the composition and richness of the weed community, with the declining in abundance of some species, and the increase in others (Vitta *et al.* 2004; de la Fuente *et al.* 2006). In many agroecosystems, these changes were correlated to reductions in food availability, mainly in winter, among other supporting services to biodiversity (Marshall *et al.* 2003). Consequently, some rodent species showed a decreasing trend in their abundance in the last decades, especially those species that are mainly present in cropfields (Fraschina *et al.* 2012).

The rodent community is characterized by the numerical dominance of *Akodon azarae* which is typically found in cropfield edges, and *Calomys laucha* which is more abundant in crops. Studies about habitat selection of these species showed that more than 90% of captures of *A. azarae* occurred in cropfield edges, but its habitat distribution varies according to the season and plant structure in both cropfields and

edges (Busch *et al.* 2001). *Calomys laucha* is more frequently captured in cropfields (Busch *et al.* 2001; Miño *et al.* 2001). Another rodent species that are present in smaller numbers, and there are more frequent in cropfield edges, are sigmodontines as *Calomys musculinus*, *Oligoryzomys flavescens*, *Oxymycterus rufus* and *Holochilus vulpinus*. There is also one native caviomorph, *Cavia aperea*. Exotic rodent species, commensal murines as *Mus musculus*, *Rattus rattus* and *Rattus norvegicus*, are abundant near human dwellings, dairy farms, pig farms and poultry farms. In contrast to rural areas of Australia, in Pampas systems commensal species are rare in cropfields and their edges, probably because of competition with native species (Busch *et al.* 2005; Miño *et al.* 2007; Fraschina *et al.* 2017). Also, in comparison to common voles in Europe, rodent species in these agroecosystems do not reach pest densities, and probably have less effect on crops because their diet is composed by a great proportion of insects, as well as seeds and other parts of plants (Ellis *et al.* 1997).

Although there are many studies about the population ecology of these species in the pampean region, the effect on their abundance of weather, vegetation, land use and predation were not previously assessed simultaneously.

In this work we want to assess the effect of weather factors, vegetation structure, predation and agrarian labours on two small rodents, *A. azarae* and *C. laucha*, abundance variations at small temporal (3 years, seasonal) and spatial scales in a pampean agroecosystem (Buenos Aires province, Argentina).

The hypotheses being tested were:

1. The abundance of both species is affected by temperature and precipitation variations.
2. Border plant cover and height affects *A. azarae* abundance in borders.
3. The abundance of *C. laucha* is affected by both border characteristics as well as by the type and stage of crops.
4. The effect of predation by the *Leopardus geoffroyi* and *Tyto furcata* on rodent abundance is higher than the effect of *Athene cunicularia*, because the latter is a generalist and opportunistic predator of rodents while the formers are specialists. Moreover, it can be expected a positive association between predation rate by *A. cunicularia* and rodent abundance."

METHODS

Study area

Field work was conducted in agroecosystems of Exaltación de la Cruz Department (34°19'S and 59°14'W), Buenos Aires province, Argentina. The study area is located in the

Rolling Pampas, an ecoregion that includes part of Buenos Aires, Córdoba and Santa Fe provinces, within banks of La Plata and Paraná rivers at northeast, Salado river at southwest and Matanza river at southeast. This region presents a highly rolling topography in comparison with other neighbour areas, forming an exoreic drain system (Bilenca & Miñarro 2004). The climate is sub-humid temperate, with a mean annual temperature of 16°C and an annual precipitation of approximately 1000 mm. Originally, the area was covered by grasslands, with a vegetation structure that corresponded to a prairie in humid years and pseudo-steppe or steppe during dry years (Soriano *et al.* 1991). The vegetation was represented by tall perennial grasses, as *Nassella* spp. [(Trin.) E. Desv.] and *Piptochaetium* spp. (J. Presl.). Nowadays 90% of the land is devoted to crops as soybean, wheat, corn and sunflower (Viglizzo *et al.* 2001; Paruelo *et al.* 2005), so the landscape is a matrix of cropfields (covering more than 95% of the area) with grassland corridors along their edges (borders) and small woodlots with a mixture of exotic and native tree species (Fraschina *et al.* 2012). Changes in plant phenology and in the stage of development of crops cause seasonal qualitative and quantitative variations in resources, both in cropfields and borders. The borders have abundant vegetation cover throughout the year, while cropfield cover varies from low levels after ploughing and sowing to high cover when crops are mature (Busch *et al.* 1997; Hodara & Busch 2006).

According to previous studies (Bellocq 1987, 1988, 1998; Bellocq & Kravetz 1994; Guidobono *et al.* 2016) the most frequent rodent predators are the *L. geoffroyi*, *T. fuscata* and *A. cunicularia*. Jaksic and Meserve (1993), Korfanta *et al.* (2005) and Pereira *et al.* (2006), found that these predators are resident and in consequence may exert an effect on their prey all along the year. Another potential

rodent predator, *Lycalopex gymnocercus*, is an omnivorous and opportunistic predator that consumes mainly fruits (Schalk & Morales 2012), and in lower proportions arthropods, mammals, birds, reptiles and amphibians (Lucherini & Luengos Vidal 2008; Varela *et al.* 2008; Schalk & Morales 2012).

Study design

We conducted a longitudinal sampling in three cropfields and their borders. All sites were neighbouring to other crop or livestock fields. Implanted crops in summer were soybean and maize, while during winter in most cases fields were without plant cover, except in one occasion in which wheat was planted.

Rodent samplings

Rodent populations were sampled at three sites including cropfields and their borders at 45 days intervals for 3 years (November 2008–December 2011). The studied sites were selected in order to ensure the continuity of the study and were separated by more than 200 m to ensure independence among them because rodents infrequently travel this distance (León *et al.* 2007; Kittlein 2009). At each site, three lines of 25 Sherman live traps ($8 \times 9 \times 23$ cm) were placed, one along the borders and two parallel lines within cropfields, perpendicular to the first and the last border trap respectively (Figure 1). The distance between traps in each line was 10 m. The distance between the first trap in the cropfield and the trap-line in the border was 20 m (Figure 1). Traps were baited with a mix of peanut butter, bovine fat and rolled oats and were checked every morning for three consecutive days. Each captured animal was



Fig. 1. Rodent sampling design. Three lines of 25 Sherman traps were placed in each one of the three sampling sites. One line was placed along the border and two in parallel lines in the cropfield. Distance between traps in each line was 10 m.

identified to species and sex. Reproductive status, corporal length, body weight, trap location and date of capture were recorded for all individuals. Rodents were given an individual mark by ear tags. Finally, they were released at the site of capture.

Precipitation and temperature records

Meteorological data were recorded placing temperature and humidity dataloggers at each cropfield (HOBO; Hepta Instruments) and from databases published online – with prior permission of the publishers (www.tutiempo.net/Buenos Aires/). We calculated the accumulated precipitation and the daily mean minimum and maximum temperatures for the 45 days period before each sampling.

Cover, height and type of vegetation in the two habitat types

The green and total plant cover (%), crop height and border plant height were recorded at each site. The type and stage of crops, when present, were also recorded.

Predation rates

Sampling of *L. geoffroyi* scats and owl pellets was carried out simultaneously with rodent samplings. Search of *L. geoffroyi* latrines and scats was conducted within woodlots near the trapping sites of rodents. Scats were assigned to *L. geoffroyi* by size and form, since there are no other wild felids with similar weight and aspect in northern Buenos Aires province (for more details, see Guidobono *et al.* 2016). *A. cunicularia* pellets were collected from burrows, or searching close to perches or individuals. Pellets of *T. furcata* were found under trees in woodlots. Additionally, pellets were collected in refuges such as water tanks and attics of houses. To ensure the origin of pellets, they were collected in sites where individuals were observed.

The number of rodent preys per pellet or scat was determined from the number of jaws and teeth found in them. We could not differentiate *C. laucha* and *C. musculus* remains, but we considered that they mainly corresponded to *C. laucha*, because *C. musculus* was rarely captured along the study (for methodological details see Guidobono *et al.* 2016).

Data analysis

In order to analyse the effect of environmental factors on rodent abundance generalized linear mixed models (GLMM), using the package lme4 (Bates *et al.* 2017), with binomial error structure, a log-link function and the Laplace approximation method were used (Bolker *et al.* 2009; Zuur *et al.* 2009; Crawley 2012). The ‘MuMIn’ package (Bartoń 2017) was used in order to adjust models containing all possible combination of the explanatory variables, including some interactions (Candidate models). The number of parameters included in each candidate model was limited by the number of cases used for each model (Burnham & Anderson 2002). Null models for each rodent

species were also constructed. In order to avoid redundancies, we estimated collinearity between main effects by means of the variance inflation factor (VIF) customized to mixed models (Schweinberger 2014). According to Zuur *et al.* (2010), $VIF < 3$ indicate absence of collinearity. For variables that showed VIF values > 3 , we conducted pairwise correlations using the package stats (R Core Team and Contributors Worldwide 2017) in order to find the correlated variables. A combination of site-month-year as a random effect was used in order to correct over-dispersion when the dispersion factor was larger than 1.5 (Harrison 2015). We applied an information-theoretic approach to selection of models and estimators (Burnham & Anderson 2002). Akaike’s information criterion with correction for small sample size (AICc) was used to rank candidate models (Burnham & Anderson 2002). The best model had the smallest value of AICc (Burnham & Anderson 2002). We also computed w_i as the weight of evidence in favour of model i being the best model in the candidate set (Akaike’s weights). We also considered all other models with AICc values smaller than those of the null model (Symonds & Moussalli 2011), and with a $\Delta AICc$ lower than 2 in relation to the best model (Richards 2005) to be supported by the data. Selected models were averaged to obtain a final model using the model averaging function (Symonds & Moussalli 2011; Bartoń 2017; R Core Team and Contributors Worldwide 2017). The magnitude of the effect of explanatory variables on rodent abundance variations was assessed through their relative importance value (the sum of weights of the models where the variable is included) and through the limits of the confidence intervals of the estimator (a variable contributes to explain abundance variations when the confidence interval of the estimator does not include the zero). In order to determine the difference between levels of categorical explanatory variables post-hoc tests were conducted using the multcomp package (Hothorn *et al.* 2017). The interaction of two continuous explanatory variables was explored with a simple slopes analysis using the jtools package (Long 2018). Finally, following Midgley *et al.* (2003), the performance of each candidate model was assessed through the ‘explained deviance (ED)’, estimated as: $1 - (\text{residual deviance}/\text{null deviance})$. Models were adjusted using overall rodent abundance, abundance in borders and abundance in cropfields, separately. All analyses were carried out using the R statistical software (R Development Core Team 2017).

The abundance of each species at each site was estimated by the Trap Success: Number of individuals captured/(number of traps \times number of nights). We estimated an overall Trap Success for both cropfields and borders (TS_o), and a Trap Success for borders (TS_b) and cropfields (TS_c) separately.

Taking in account that we could not estimate predator abundances, as a proxy of predation rate, we estimated the mean number of rodents found per pellet or scat for each predator (total number of rodents found divided by the number of pellets or scats), rodent species, and sampling period. In consequence, we assumed that main variations in predation rate were related to individual consumption rather than to variations in predator numbers.

Explanatory variables for both species were: year as a three-level fixed factor (2009, 2010 and 2011), season as a four-level fixed factor (spring, summer, autumn and winter),

accumulated precipitation, daily mean minimum temperature, daily mean maximum temperature, *L. geoffroyi* predation rate, *T. fuscata* predation rate, *A. cunicularia* predation rate, cropfield use as a six-level fixed factor (corn, weeds, implanted pasture, soybean, bare soil and wheat), stage of crops as a four-level fixed factor (initial, intermediate, mature and stubble), total and green plant cover of cropfield, total and green plant cover of borders, crop height and border plant height. We also included as explanatory variables, for *A. azarae*: *C. laucha* TS_o , TS_b and TS_c , and for *C. laucha*: *A. azarae* TS_o , TS_b and TS_c . All main effects were calculated considering a 45-day period before the sampling in which the response variable was recorded. We also considered delayed effects, relating the response variable to environmental factors evaluated between 45 and 90 days (delay 1) and between 90 and 135 days (delay 2) before the corresponding rodent sampling.

RESULTS

Rodent samplings

A total of 511 individuals were captured with a trapping effort of 16 200 Sherman trap-nights. Captured rodents included native sigmodontines: *A. azarae* ($n = 333$), *C. laucha* ($n = 109$), *O. flavescens* ($n = 30$), *C. musculus* ($n = 27$) and *O. rufus* ($n = 7$), one caviid: *C. aperea* ($n = 2$) and two species of introduced murines: *R. norvegicus* ($n = 2$) and *M. musculus* ($n = 1$). In border habitats all rodent species described were trapped, *A. azarae* was the most frequently trapped species, representing 77% of the captures, *C. laucha* and *O. flavescens* represented 7% of the captures each, while *C. musculus* represented 6% of the captures. *O. rufus* represented only the 2% of captures and *M. musculus*, *R. norvegicus* and *C. aperea*, combined, represented the remaining 2% of the captures. In cropfields only four rodent species were captured, *C. laucha* was the most frequent species, representing 75% of the captures, *A. azarae* represented 18% of the captures (being trapped in trap stations near borders), *C. musculus* represented 5% of the captures and *O. flavescens* represented the remaining 2% of the captures.

Effect of environmental factors on rodent abundance

Akodon azarae

For this species, we only adjusted models using TS_o and TS_b because numbers in cropfields were not enough to adjust models. After the GLMM analysis, the best model had a ΔAIC value with respect to the null model of 256.25, while other six models had

$\Delta AIC < 2$ with respect to the best model. According to the average model, variables with the highest relative importance values (1.00) were cropfield plant height, green plant cover in borders with delay 1, border plant height with delay 2 and season. Cropfield height had a positive effect on overall *A. azarae* abundance, while green plant cover had a negative effect. Confidence intervals of the last variable included zero values, and in consequence its effect is not important. The effect of the border plant height with delay 2 on *A. azarae* abundance showed an interaction with the season (relative importance value = 0.91), with a highest positive effect on *A. azarae* abundance in summer, suggesting that high vegetation in borders in spring favours an increase in abundance in summer. Predation rate of *T. fuscata* with delay 2 (in the previous season) had a negative effect on *A. azarae* abundance, but with a lower relative importance (0.75) and with zero values included in its confidence interval. Relative importance of the other variables were low (Table 1).

For the abundance of *A. azarae* in borders were included 13 models with $\Delta AIC < 2$ with respect to the best model. The average model showed the importance of the cropfield height with delay 2 and the interaction between border height with delay 2 and the season (relative importance = 1), as for the overall abundance of *A. azarae*. The other variables showed relative importance values < 0.7 (Table 2).

Calomys laucha

For this species we adjusted models for the overall abundance (TS_o), abundance in cropfields (TS_c) and in borders (TS_b). For TS_o , 14 models with $\Delta AIC < 2$ with respect to the best model were included. According to the average model, the season was the best variable to explain *C. laucha* abundance variations, with the highest abundance in summer (relative importance = 1.00, Table 3). The effect of predation rate by *L. geoffroyi* (positive) and *T. fuscata* (negative) showed relative importance values of 0.49 and 0.63, but the confidence intervals included the zero. Interactions of variables also showed low relative importance values, although confidence intervals of the interaction between *L. geoffroyi* and *T. fuscata* predation rates did not include zero (Table 3).

For *C. laucha* abundance in fields eight models were selected. According to the average model, the season was again the best variable to explain abundance variations, showing the highest abundance in summer (relative importance = 1, Table 4). Green plant cover in borders had a negative effect on *C. laucha* abundance in fields (relative importance = 0.86), suggesting that individuals of this species move between habitats according to their relative conditions. Predation rate by *T. fuscata* had a relative

Table 1. Candidates and average models for *Akodon azarae* overall abundance variations (TS_o)

	Candidate models														RVI	Average model	
	1		2		3		4		5		6		7			Estimator	SE
	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE			
Intercept	-3.24	0.54	-2.07	0.86	-3.32	0.56	-1.82	0.86	-2.28	0.87	-3.09	0.54	-2.25	0.59		-2.64	0.91
Bh.2	0.61	0.39	-0.66	0.82	0.55	0.40	-0.85	0.81	-0.58	0.84	0.53	0.39	-0.55	0.53	1.00	-0.07	0.88
Ch.1	0.81	0.24	0.76	0.24	0.84	0.25	0.67	0.24	0.80	0.25	0.74	0.25	0.62	0.25	1.00	0.76	0.25
gcB.1	-1.07	0.42	-2.67	1.03	-0.96	0.43	-2.86	1.02	-2.37	1.04	-1.14	0.42	-2.60	0.86	1.00	-1.88	1.10
Spring	-0.79	0.61	-0.90	0.62	-0.97	0.62	-0.70	0.62	-1.08	0.62	-0.62	0.61	-1.39	0.32	1.00	-0.90	0.63
Summer	-3.02	0.69	-3.13	0.68	-2.96	0.70	-2.98	0.66	-3.05	0.69	-2.87	0.68	-1.71	0.30	1.00	-2.91	0.74
Winter	-0.27	0.70	-0.95	0.79	-0.43	0.72	-1.03	0.77	-1.03	0.81	-0.30	0.69	-0.97	0.30	1.00	-0.67	0.78
TfP.2	-0.55	0.29	-0.59	0.28			-1.70	0.85			-1.51	0.86	-0.86	0.36	0.75	-0.91	0.62
Bh.2 × Spring	-1.35	1.07	-1.54	1.11	-1.33	1.09	-1.66	1.10	-2.28	0.87	-1.43	1.05			0.91	-1.46	1.10
Bh.2 × Summer	1.57	0.62	1.66	0.61	1.38	0.63	1.53	0.60	-0.58	0.84	1.44	0.61			0.91	1.53	0.62
Bh.2 × Winter	-0.77	0.56	-0.05	0.69	-0.70	0.58	-0.01	0.67	0.80	0.25	-0.78	0.55			0.91	-0.42	0.72
Bh.2 × gcB.1			1.83	1.06			1.95	1.04	1.62	1.08			1.95	0.86	0.52	1.83	1.03
Bh.2 × TfP.2							0.98	0.70			0.86	0.72			0.22	0.92	0.71
Ch.1 × TfP.2													1.24	0.57	0.09	1.24	0.57
ED	0.90		0.89		0.90		0.89		0.89		0.89		0.89				
Log-likelihood	-173.72		-172.24		-175.67		-171.26		-174.54		-173.01		-176.20				
AICc	379.72		379.85		380.62		381.10		381.35		381.39		381.68				
ΔAICc	0.00		0.13		0.90		1.38		1.63		1.67		1.96				
w _i	0.23		0.22		0.15		0.12		0.10		0.10		0.08				

Explanatory variables were: border plant height with delay 2 (Bh.2), crop height with delay 1 (Ch.1), green plant cover of borders with delay 1 (gcB.1), *Tyto furcata* predation rate with delay 2 (TfP.2), season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance (RVI), explained deviance (ED), the maximized log-likelihood, Akaike's information criterion corrected for small sample size (AICc), difference between the AICc of the best model and the AICc of model_i (ΔAICc) and Akaike's weights (w_i). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 635.97.

Number of estimable parameters in the global model: 19.

importance of 0.64, and confidence intervals included zero. The interaction between *T. furcata* and *L. geoffroyi* predation rates had a low value of relative importance, but confidence intervals did not include the zero (Table 4).

This interaction, although with low relative importance, was included in both TS_o and TS_c *C. laucha* models. According to the simple slope analysis, predation rate of *T. furcata* has a negative effect on *C. laucha* overall abundance when *L. geoffroyi* predation rates are lower than the mean (Table 5). This analysis was conducted, as an example, for the best model (model 1) of overall abundance, because estimators and standard errors were similar in other models where this interaction appeared.

To describe the changes in abundance of *C. laucha* in borders (TS_b), eight models were selected. According to the average model, only the cropfield plant height with delay 2 had a high relative importance (0.92) on *C. laucha* abundance in borders with a positive effect. The effect of season had a low value of relative importance (0.18), but according to the

confidence intervals, in winter and spring the abundances were lower than in autumn (Table 6).

DISCUSSION

Small mammals are strongly affected by environmental conditions at different temporal and spatial scales. In agrarian systems periodic changes in habitat conditions due to farming practices affect the availability of food and cover (Jacob 2003) at both small temporal and spatial scales. The effect of environmental conditions may differ among species in a community (Lima *et al.* 2002). According to our expectations, in our study the effect of environmental factors differed between the two rodent species, but, contrary to our hypotheses, *A. azarae* abundance was influenced not only by border characteristics but also by cropfield features. We did not detect a direct effect of meteorological variables, but they probably influenced indirectly through the vegetation and its effect was also expressed in the effect of seasons on *C. laucha*. This

Table 2. Candidate models for *Akodon azarae* abundance variation in borders (TS_b)

	Candidate models													
	1		2		3		4		5		6		7	
	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE
Intercept	-2.92	0.39	-2.45	0.47	-1.39	0.76	-3.05	0.40	-1.27	0.76	-3.09	0.54	-2.60	0.48
Bh.2	0.66	0.32	0.61	0.32	-0.56	0.74	0.49	0.32	-0.59	0.74	0.53	0.39	0.43	0.32
Ch.1	0.59	0.22	0.62	0.22	0.60	0.21	0.67	0.23	0.58	0.21	0.74	0.25	0.70	0.23
tcC	-0.52	0.27	-0.54	0.27	-0.54	0.26			-0.57	0.26				
Spring	-0.93	0.54	-1.04	0.55	-1.16	0.57	-1.24	0.53	-1.00	0.58	-0.62	0.61	-1.35	0.55
Summer	-2.96	0.68	-3.04	0.68	-3.14	0.67	-3.46	0.65	-3.17	0.66	-2.87	0.68	-3.55	0.65
Winter	0.24	0.58	-0.04	0.60	-0.68	0.69	-0.18	0.56	-0.63	0.69	-0.30	0.69	-0.47	0.60
TfP.2									-0.40	0.24	-1.51	0.86		
gcB.1			-0.63	0.39	-2.13	0.97			-2.35	0.98	-1.14	0.42	-0.61	0.40
Bh.2 × gcB.1					1.74	1.00			1.89	1.00				
Ch.1 × tcC														
Bh.2 × Spring	-1.06	0.98	-1.11	1.03	-1.27	1.12	-0.91	1.00	-1.34	1.13	-1.43	1.05	-0.95	1.06
Bh.2 × Summer	1.49	0.55	1.58	0.55	1.64	0.54	1.78	0.55	1.78	0.54	1.44	0.61	1.88	0.55
Bh.2 × Winter	-1.02	0.47	-0.95	0.47	-0.27	0.60	-0.77	0.47	-0.25	0.59	-0.78	0.55	-0.69	0.48
Bh.2 × TfP.2											0.86	0.72		
ED		0.80		0.81		0.80		0.81		0.81		0.85		0.82
Log-likelihood	-144.72		-143.45		-141.97		-146.49		-140.46		-142.20		-145.32	
AICc	318.81		319.17		319.32		319.39		319.49		319.78		319.93	
ΔAICc	0.00		0.36		0.51		0.58		0.68		0.97		1.12	
w _i	0.13		0.11		0.10		0.10		0.09		0.08		0.07	

	Candidate models												Average model		
	8		9		10		11		12		13				
	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	RVI	Estimator	SE
Intercept	-2.94	0.38	-1.57	0.78	-1.10	0.74	-1.23	0.74	-1.45	0.78	-3.07	0.40		-2.19	0.91
Bh.2	0.72	0.32	-0.72	0.75	-0.75	0.71	-0.90	0.75	-0.75	0.75	0.54	0.32	1.00	0.07	0.80
Ch.1	0.57	0.22	0.67	0.22	0.51	0.21	1.17	0.45	0.66	0.22	0.65	0.22	1.00	0.64	0.25
tcC	-0.54	0.27			-0.51	0.25	-0.05	0.43					0.68	-0.50	0.29
Spring	-0.80	0.55	-1.44	0.57	-0.82	0.58	-1.11	0.58	-1.32	0.58	-1.12	0.54	1.00	-1.08	0.59
Summer	-2.96	0.67	-3.65	0.65	-3.06	0.65	-3.34	0.66	-3.70	0.65	-3.48	0.64	1.00	-3.23	0.71
Winter	0.36	0.58	-1.08	0.69	-0.72	0.67	-1.08	0.73	-1.06	0.69	-0.08	0.56	1.00	-0.33	0.77
TfP.2	-0.32	0.24			-1.53	0.77	-0.45	0.24	-0.38	0.24	-0.29	0.24	0.44	-0.53	0.42
gcB.1			-2.07	0.98	-2.45	0.96	-2.72	1.00	-2.27	0.99			0.66	-1.66	1.15
Bh.2 × gcB.1			1.70	1.03	1.96	0.98	2.17	1.00	1.84	1.03			0.41	1.86	1.02
Ch.1 × tcC							-0.88	0.59					0.05	-0.88	0.59
Bh.2 × Spring	-1.10	0.98	-1.15	1.14	-1.45	1.12	-1.36	1.15	-1.20	1.15	-0.94	1.00	1.00	-1.14	1.07
Bh.2 × Summer	1.58	0.55	1.93	0.54	1.65	0.53	1.96	0.55	2.07	0.55	1.87	0.55	1.00	1.72	0.57
Bh.2 × Winter	-1.05	0.47	-0.04	0.61	-0.19	0.57	0.08	0.61	-0.003	0.60	-0.80	0.47	1.00	-0.60	0.65
Bh.2 × TfP.2					0.97	0.62							0.06	0.97	0.62
ED		0.81		0.82		0.80		0.79		0.82		0.82			
Log-likelihood	-143.85		-143.98		-139.23		-139.40		-142.71		-145.76				
AICc	319.97		320.23		320.35		320.69		320.79		320.80				
ΔAICc	1.16		1.42		1.54		1.88		1.98		1.99				
w _i	0.07		0.06		0.06		0.05		0.05		0.05				

Explanatory variables were: border plant height with delay 2 (Bh.2), crop height with delay 1 (Ch.1), total cover of crop-fields (tcC), green plant cover of borders with delay 1 (gcB.1), *Tyto furcata* predation rate with delay 2 (TfP.2), season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance (RVI), explained deviance (ED), the maximized log-likelihood, Akaike's information criterion corrected for small sample size (AICc), difference between the AICc of the best model and the AICc of model_{*i*} (ΔAICc) and Akaike's weights (w_i). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 510.23.

Number of estimable parameters in the global model: 16.

Table 3. Candidate models for *Calomys laucha* overall abundance variations (TS₀)

	Candidate models													
	1		2		3		4		5		6		7	
	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE
Intercept	-5.84	0.57	-5.85	0.38	-6.06	0.41	-5.76	0.39	-4.59	1.51	-4.24	1.70	-6.17	0.50
Ch.2	-0.16	0.49												
Ap									-8.47	12.29	-10.60	12.78	3.18	2.31
gcB														
Spring	-0.26	0.63	-0.82	0.58	-0.90	0.59	-0.70	0.57	-4.03	1.99	-4.05	2.10	-0.72	0.56
Summer	1.34	0.50	0.84	0.49	0.89	0.48	1.03	0.46	-0.47	1.61	-0.57	1.75	0.75	0.49
Winter	-1.48	0.84	-1.29	0.63	-1.78	0.72	-1.86	0.77	1.52	2.14	3.97	2.57	-1.87	0.76
TfP.2	-3.44	1.17					-1.66	0.84	-1.31	0.70	-2.95	1.04	-1.60	0.81
LgP.1	0.46	2.27			3.28	2.15	1.07	2.32					1.60	2.30
Ch.2 × TfP.2	5.53	2.24									5.15	2.17		
LgP.1 × TfP.2	12.30	4.05					7.57	3.44					7.70	3.35
Ap × Spring									28.02	14.91	30.33	15.32		
Ap × Summer									10.34	12.50	12.65	13.10		
Ap × Winter									-28.85	19.39	-49.56	22.34		
Ch.2 × LgP.1														
ED	0.83		0.84		0.84		0.83		0.80		0.80		0.82	
Log-likelihood	-91.20		-97.91		-96.72		-94.18		-91.61		-88.85		-93.25	
AICc	208.80		209.11		209.20		209.27		209.63		209.97		210.11	
ΔAICc	0.00		0.31		0.40		0.47		0.83		1.17		1.31	
w _i	0.12		0.10		0.10		0.10		0.08		0.07		0.06	

	Candidate models														Average model		
	8		9		10		11		12		13		14				
	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	RVI	Estimator	SE
Intercep	-6.12	0.60	-6.45	0.52	-5.41	0.54	-4.78	1.59	-5.37	0.70	-5.24	0.58	-6.01	0.59		-5.60	0.89
Ch.2	-0.25	0.48							-0.15	0.49			0.21	0.59	0.35	-0.16	0.52
Ap			3.06	2.45			-8.05	12.89							0.38	-1.26	1.45
gcB					-1.09	0.99			-1.02	0.96	-1.15	0.98			0.15	-1.09	0.98
Spring	-0.39	0.62	-0.90	0.58	-0.45	0.67	-4.25	2.03	0.05	0.70	-0.30	0.66	-0.27	0.63	1.00	-1.26	1.45
Summer	1.03	0.54	0.63	0.51	1.22	0.59	-0.50	1.69	1.67	0.60	1.42	0.57	1.42	0.51	1.00	0.77	0.93
Winter	-1.59	0.83	-1.75	0.70	-1.33	0.63	-0.64	1.87	-1.47	0.84	-1.85	0.77	-1.65	0.87	1.00	-0.95	1.55
TfP.2	-3.31	1.14							-3.49	1.19	-1.73	0.85	3.39	1.16	0.63	-2.52	1.34
LgP.1	0.97	2.25	3.82	2.16					-0.31	2.37	0.22	2.41	2.56	3.04	0.49	1.53	2.66
Ch.2 × TfP.2	5.28	2.19							5.42	2.25			5.67	2.22	0.35	5.42	2.22
LgP.1 × TfP.2	12.21	3.93							12.97	4.15	8.41	3.54	11.45	4.08	0.49	10.36	4.40
Ap × Spring							27.70	15.46							0.20	28.71	15.24
Ap × Summer							9.84	13.11							0.20	11.00	12.92
Ap × Winter							-10.50	17.08							0.20	-31.07	24.60
Ch.2 × LgP.1													6.66	6.52	0.05	-6.66	6.52
ED	0.82		0.83		0.84		0.81		0.83		0.83		0.83				
Log-likelihood	-90.43		-95.96		-97.30		-93.44		-90.63		-93.48		-90.68				
AICc	210.15		210.21		210.36		210.50		210.56		210.57		210.65				
ΔAICc	1.35		1.41		1.56		1.70		1.76		1.77		1.85				
w _i	0.06		0.06		0.06		0.05		0.05		0.05		0.05				

Explanatory variables were: crop height with delay 2 (Ch.2), accumulated precipitation (Ap), green plant cover of borders (gcB), *Tyto furcata* predation rate with delay 2 (TfP.2), *Leopardus geoffroyi* predation rate with delay 1 (LgP.1), season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance (RVI), explained deviance (ED), the maximized log-likelihood, Akaike's information criterion corrected for small sample size (AICc), difference between the AICc of the best model and the AICc of model_i (ΔAICc) and Akaike's weights (w_i). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 298.68.

Number of estimable parameters in the global model: 16.

last effect, however, may also be a consequence of changes in crop stages, not only of temperature or precipitation variations through seasons. Green plant

cover on borders had a negative effect on *C. laucha* abundance in fields, suggesting that this species changes its habitat distribution depending on relative

Table 4. Candidates and average models for *Calomys laucha* abundance variations in cropfields (TS_c)

	Candidate models																Average model			
	1		2		3		4		5		6		7		8					
	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	RVI	Estimator	SE	
Intercept	-5.52	0.87	-5.10	0.90	-3.56	2.95	-5.65	2.61	-5.43	0.86	-5.83	0.94	-5.84	0.95	-5.59	1.02		-5.18	1.62	
Ap					-14.34	22.59	-5.03	20.94					3.05	3.52			0.46	-5.65	18.24	
gcB	-3.89	1.79	-3.79	1.72	-2.79	1.65			-3.89	1.78	-3.53	1.80	-3.99	1.80	-3.72	1.71	0.86	-3.62	1.79	
Spring	1.49	1.18	1.84	1.14	-7.14	4.91	-8.55	5.12	1.68	1.19	1.29	1.19	1.51	1.17	1.74	1.13	1.00	-1.25	4.65	
Summer	3.83	1.16	3.98	1.08	1.27	2.81	1.54	2.68	3.89	1.15	3.73	1.15	3.62	1.18	3.68	1.10	1.00	3.08	1.93	
Winter	-0.44	1.01	-0.69	1.14	3.84	3.80	4.91	3.58	-0.18	1.03	-0.78	1.09	-0.35	1.00	-0.74	1.12	1.00	0.94	2.80	
TfP.2			-3.45	1.56	-2.59	1.26	-2.54	1.22	-0.79	0.91					-3.21	1.50	0.64	-2.67	1.54	
LgP.1			-1.16	3.50							2.84	3.28			-0.12	3.59	0.34	0.04	3.82	
LgP.1 × TfP.2			13.75	5.83													0.26	13.57	5.78	
Ap × Spring					60.05	31.71	60.69	32.46									0.30	60.34	32.05	
Ap × Summer					16.31	22.93	5.94	21.13									0.30	11.67	22.72	
Ap × Winter					-40.50	32.87	-48.25	30.98									0.30	-43.96	32.26	
ED	0.91		0.90		0.88		0.87		0.91		0.91		0.91		0.89					
Log-likelihood	-68.84		-65.01		-62.23		-63.89		-68.46		-68.47		-68.47		-64.48					
AICc	153.44		153.63		153.75		154.18		155.21		155.22		155.23		155.36					
ΔAICc	0.00		0.19		0.31		0.74		1.77		1.78		1.79		1.92					
w _i	0.20		0.18		0.17		0.14		0.08		0.08		0.08		0.08					

Explanatory variables were: accumulated precipitation (Ap), green plant cover of borders (gcB), *Tyto furcata* predation rate with delay 2 (TfP.2), *Leopardus geoffroyi* predation rate with delay 1 (LgP.1), season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance in candidate models (RVI), explained deviance (ED), the maximized log-likelihood, Akaike's information criterion corrected for small sample size (AICc), difference between the AICc of the best model and the AICc of model_i (ΔAICc) and Akaike's weights (w_i). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 261.52.

Number of estimable parameters in the global model: 14.

environmental conditions in both habitats. Our analysis was focused on short temporal effects on rodent abundance, while in a long-term (24 years) study, Frascina *et al.* (2012) found a direct effect of temperature and precipitation on *A. azarae* and *C. laucha* abundance, highlighting that rodent population dynamics is affected by multiple factors that operate at different spatial and temporal scales. Andreo *et al.* (2009b) also found lagged effects of precipitation and NDVI (a proxy of vegetation cover) on *A. azarae* abundance in longitudinal habitats of rural areas of central Argentina.

The abundance of both species was affected by characteristics of cropfields and borders, suggesting that, although each species is more abundant in one habitat (*A. azarae* in borders and *C. laucha* in fields), they use both habitats. For example, a mature and tall crop enhances the increase of overall *A. azarae* abundance that is expressed 45 days later, while border plant height has also a positive effect but only in summer. In Europe, recommendations to farmers for the decrease in *Microtus arvalis* abundance (which can reach pest levels in crops) is partly based on the effect of plant height on rodent abundance (Jacob *et al.* 2014).

Table 5. Simple slope analysis of the interaction between *Tyto furcata* and *Leopardus geoffroyi* predation rates using the best model (candidate model 1) for the overall abundance of *Calomys laucha*

	LgP.1 = 0.2 (+1 SE)	LgP.1 = 0.09 (mean)	LgP.1 = -0.02 (-1 SE)
Estimator	0.85	-0.5	-1.86
SE	0.65	0.65	0.91

Three values of *L. geoffroyi* predation rate were fixed (mean, mean + standard error, mean - standard error) to test the association between *T. furcata* predation rate and the abundance of *C. laucha*. Table entries state the corresponding statistics: Estimator of the association with the explanatory variable, standard error of the estimator (SE). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

According to our results, the management of both species, *A. azarae* and *C. laucha*, may take into account both habitats because their use is dynamic and varies depending on their relative conditions, the season, rodent abundance and interspecific competition between both species. This dynamic change in distribution between fields and margins according to

Table 6. Candidates and average models for *Calomys laucha* abundance variations in borders (TS_b)

	Candidate models																RVI	Average model	
	1		2		3		4		5		6		7		8			Estimator	SE
	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE	Estimator	SE			
Intercept	-6.42	0.42	-6.55	0.58	-6.31	0.49	-6.49	0.49	-6.40	0.50	-6.45	0.67	-5.42	0.55	-4.83	0.37		-6.20	0.66
Ch.2	1.41	0.42	1.39	0.42	1.19	0.46	1.45	0.45	1.40	0.44	1.41	0.42	0.77	0.45			0.92	1.32	0.47
Ap			0.92	2.79													0.10	0.92	2.79
gcB											0.05	0.86					0.10	0.05	0.86
Spring													-1.26	0.72	-1.74	0.67	0.18	-1.48	0.74
Summer													-0.34	0.51	-0.64	0.49	0.18	-0.48	0.52
Winter													-1.55	0.86	-2.15	0.78	0.18	-1.83	0.88
TtP.2					-0.45	0.85	0.18	0.65									0.21	-0.14	0.82
LgP.1									-0.14	2.35							0.10	-0.14	2.35
Ch.2 × TtP.2					2.86	1.84											0.10	2.86	1.84
ED		0.52		0.53		0.51		0.52		0.52		0.52		0.44		0.45			
Log-likelihood		-55.53		-55.47		-54.28		-55.49		-55.53		-55.53		-53.12		-54.49			
AICc		119.70		121.90		121.91		121.93		122.01		122.01		122.03		122.31			
ΔAICc		0.00		2.20		2.21		2.23		2.31		2.31		2.33		2.61			
w _i		0.31		0.10		0.10		0.10		0.10		0.10		0.10		0.08			

Explanatory variables were: crop height with delay 2 (Ch.2), accumulated precipitation (Ap), green plant cover of borders (gcB), *Tyto furcata* predation rate with delay 2 (TtP.2), *Leopardus geoffroyi* predation rate with delay 1, season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance in candidate models (RVI), explained deviance (ED), the maximized Log-likelihood, Akaike's information criterion corrected for small sample size (AICc), difference between the AICc of the best model and the AICc of model_i (ΔAICc) and Akaike's weights (w_i). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 261.52.

Number of estimable parameters in the global model: 14.

habitat characteristics and seasons was also observed for *M. arvalis* in Spain (Rodríguez-Pastor *et al.* 2016).

In European agroecosystems, the spillover from edge habitats of some rodent species, as *M. arvalis*, is considered a threaten to crop production. In our system, rodents never achieve pest densities as reported in Europe (>1000 voles per hectare, Jacob *et al.* 2014). In cropfield borders we found a maximum of 50 individuals of *A. azarae* per hectare (Gorosito 2018), and it is rarely captured in fields. *Calomys laucha* has even lower values of abundance both in cropfields and edges. The absence of a spillover of *A. azarae* from field margins to crops is in agreement with the observation for *M. arvalis* in an agrarian landscape in Switzerland (Briner *et al.* 2005).

This is the first report of an effect of predation rate on abundance for the studied species, but this effect was only observed for predation by *T. furcata* and had high relative importance for *A. azarae* but not for *C. laucha*. The effect of *T. furcata* on this latter species was only expressed when *L. geoffroyi* predation rates were lower than the mean and *C. laucha* abundance was probably also low. The differential effect depending on the rodent species is consistent to the hunting habits of this avian predator, which looks for prey mainly along borders (Bellocq & Kravetz 1994), where *A. azarae* is more abundant. A similar effect on rodents living in edges was observed by Figueroa *et al.* (2009) for *Oligoryzomys longicaudatus*, and was related to the sit-and-wait behaviour of

T. furcata perching in post fences. Contrary to our expectation, predation by *L. geoffroyi* had no effect on *A. azarae* abundance, and for *C. laucha*, its effect was positive and of low relative importance (0.49). Guidobono *et al.* (2016) proposed that *L. geoffroyi* consumes *C. laucha* opportunistically, increasing consumption with higher abundance, and that it prefers to hunt in open areas with low plant cover, as fields in some stages of the crop. Other authors (Bisceglia *et al.* 2008; Pereira 2010) also observed that *L. geoffroyi* shows prey shifts when resources fluctuate temporarily. Our results support the prediction that *A. cunicularia* has a lower predation effect than *T. furcata* and *L. geoffroyi*.

In summary, short-term abundance variations of both species were explained by the characteristics of the whole system, and it seems that the existence of alternative habitats which change asynchronously, allows rodent survival in a system that is strongly altered by agrarian labours, but does not produce high increases in abundance and there is no spillover of surplus individuals from margins to crops. Finally, the specialist avian predator *T. furcata* may contribute to prevent *A. azarae* population eruptions.

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